BIOPHYSICS AS A POINT OF VIEW IN PLANT PHYSIOLOGY [1]

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This year is the 300th anniversary of the appearance of Francis Bacon's "Novum Organum, or true suggestions for the interpretation of Nature." It is appropriate and perhaps not presumptuous to take as a text one of Bacon's remarks and as a subject a point of view with respect to our science, for Bacon's work was essentially the presentation of a point of view: "Francis of Verulam thought thus," he said. This text and this subject are contained in his 36th Aphorism:

> We have but one simple method of delivering our sentiments, namely, we must bring men to particulars and their regular series and order.

In other words, it is proposed that we consider the applicability of a quantitative, physical method to plant physiology: the regularity—the mathematical regularity—of the series and order of its "particulars." This applicability, indeed, is implied in the original meaning of the Greek word for physics: a knowledge of the regular successions and relations of events, whether these events be mechanical or vital. It is the Greek equivalent for the Latin word for nature, so that biophysics is but the re-charting of a field of knowledge, the traverse survey of which was made by the ancients.

Whatever one may feel regarding the utility of a purely physical point of view in plant physiology, its chief value lies in its offering *another* gateway into the unknown while closing none now existing, for the most securely based hope of progress in plant physiology rests upon the varied attitude of its votaries toward their science, a science that is unable to demand a particular viewpoint from the very nature of its subject matter. Like Bacon, I seek not to discredit the constituted authorities, or their methods, or their desires. But I do propose to call attention to certain possibilities that are not presented in the diet of reading that is regularly offered to those who are completing their apprenticeship as plant physiologists.

The physical edifice is three-storied, at least in practice. The first story, on which the others rest, is the conspicuous one to the outsider. It is the busy, experimental floor that is presided over by *Precision* and is so commonly pictured in the textbooks.

In the second story we find the models that serve to identify all physical processes regardless of where they may be encountered. With them is arranged the collection of laws, theories, and hypotheses that is constantly

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being augmented by additions from the laboratories below, and that is constantly being altered by the substitution of new items of improved design for those fabricated in the past. It is a temptation to linger here, for there are so many things reminiscent of phenomena in plant physiology. On this floor abstract reasoning is the principal activity. Details of the results achieved below-stairs are sorted, criticized, and classified. Those that are unessential are filed, and the others are built into more and more elaborate models as the skill on the part of the laboratory operatives increases and new and better machinery and tools are acquired.

But it is to the third story that the guide conducts us today. Here are quiet rooms, thick with silence, in which the faiths of a science are kept. These are stored as sketches prepared in the idle moments of genius: skeleton diagrams of the possible relations between many apparently dissimilar categories of data. Some of these diagrams may now be viewed as models on the second floor. Others have been shown to have inherent fallacies, while others are so grand in conception that an infinity of time will be required to set in final place all the details of which they hint.

The largest of these is labeled "Conceptions of the material system." So large is it that one is likely to miss the whole in contemplation of its parts, for the sketch is a patchwork of many, and the light shed by published comments is flickering, so that now one, now another part is illuminated.

It is now purposed to render one aspect of the material system, thus pictured, into concise wording and to contemplate its application to the study of the living plant.

Broadly speaking, the large, composite sketch says: "A system as a whole possesses interrelated properties that may be quantitatively investigated as such without regarding the molecular constitution of the system or the molecular kinetics of its processes, and a quantitative statement of the *laws* of a system as a rule is a helpful antecedent to all *theories* of the cause of its unique behavior." Now the recognition of the living plant as such a system is generally being only unconsciously made in plant physiology. In physical chemistry a system is sometimes defined as an aggregation of matter in, or tending towards, equilibrium. This definition is incomplete, for it makes no mention of the fact that systems possess peculiar properties that characterize the system as a whole, distinguish it from other systems, and can not be obtained by adding together the properties of its components. In general every system has certain properties characteristic only of itself and not deducible from the properties of its parts. This is true of all systems: chemical, mechanical, vital.

Let us now return to the first floor and note what Physics does. She takes systems as she finds them in nature and tries to discover a measurable feature that will serve to identify a class of systems, adjudged a class from their common behavior in some respect. She further seeks to find a number that will, by its magnitude only, indicate the degree to which an individual

system of the class is capable of manifesting the activity that identifies the class. She does this without anticipating any theory to account for the activity and without considering that, with respect to other activities, these individual systems of the class may be wholly unrelated.

It is sometimes doubted that this is done in physics. Physics is reputed to be in constant search for explanations of phenomena. That, of course, is true, and no science can abandon attempts along this line. But it is likewise true that physics does not make the search for explanation as the first step. The first step is the formulation of a quantitative law that represents the relation between the activity characteristic of the class and the quantity that symbolically represents the individual system, in other words, a constant whose magnitude may vary in any way whatever from system to system of the same class. When this law is established, the task is undertaken of discovering the law that connects the magnitude of the constant with some measurable feature of the individual system, some characteristic that can be measured when the system is not manifesting the activity under consideration or which for some other reason renders calculation of the constant easier.

Somewhere, at some time during this undertaking, an observation is made that leads an experimenter to connect the behavior of systems in one class with that of systems in another. Gradually thus relationships are perceived, the statements of which are, in fact, the so-called explanations, each law being seen to be a special case of another and "explained" by the more general. I do not mean that each individual physicist progresses in this way, but that, on the whole, this faith that careful measurement of the interrelations of activities of individual systems, the expression of the quantitative relations between the attributes of these systems, always with the view of defining the particular systems each by the magnitude of a measurable dimension, a static character, etc., or by a relation between such characters, a constant in short—faith in this method has been the keystone of progress in physics.

Because this may appear to be but the opinion of an outsider, perhaps it would be best to quote a physicist. Clerk Maxwell's classification of the physical sciences may be summarized thus:

The chief divisions of physics are two:

A. Fundamental science of dynamics, or the doctrine of the motions of bodies as affected by force.

B. Secondary physical sciences. Each has two divisions or stages. To quote:[2]

> In the elementary stage it is occupied in deducing from the observed phenomena certain general laws and then employing these laws in the calculation of all varieties of phenomena. In the dynamical stage the general laws already discovered are analyzed and shown to be equivalent to certain forms of the dynamical relations of a connected system and the attempt

[2] Maxwell, J. Clerk. Physical sciences. Encyc. Brit. **19**: 1–3. The R. S. Peale reprint of the 9th edition. Chicago, 1892.

is made to discover the nature of the dynamical systems of which the observed phenomena are the motions. The dynamical theories of the different physical sciences are in very different stages of development and in almost all of them a sound knowledge of the subject is best acquired by adopting, at least at first, the method we have called "elementary," that is to say, the study of the connection of the phenomena *peculiar to the science* without reference to *any* dynamical explanations or hypotheses.

The italics are mine.

A glance over some of these secondary sciences (which include such theoretically unrelated topics as *elasticity of figure in solids*, *viscosity*, *cohesion of liquids*, *thermodynamics*, *geometrical optics*, *electricity and magnetism*) and a perusal of a standard text on the subject must be convincing that physics does take systems as she finds them in nature and finds mathematical relationships between their conveniently measured attributes, without considering at the outset any dynamical theory to account for the properties. And, lastly, it must be noted that in the mathematical expression, the concrete, individual system is represented by one or more constants whose magnitudes are determined by independent measurements on the system itself.

It has been objected that plants are far too complicated systems to have any such constants, that the variation of one plant from another of the same species would be so great that there would be no value in the constant, that the evaluation of the constant would involve its determination for each plant and would require so much work as to defeat the object. Perhaps it is useless to discuss the matter in advance, but there are many reasons for doubting the cogency of these arguments. Indeed, the more one ponders the matter the more one is convinced that estimating the degree of potential activity of systems by inspections of their surface features is a universal method of the human race. In the affairs of life we say that one who is successful in the exercise of this method has judgment; symptomology in medicine is the systematization of the results of such an attitude.

The botanists of yesterday recorded numberless instances of morphological characters that are always found associated—or correlated, as they said. It is, of course, recognized that structure and function have some sort of interrelation, and a good deal of work has been directed toward finding the so-called causes of the interrelation. It is becoming likewise probable that a great number, at least, of physiological processes are correlated. All this would be predictable from the point of view of the physical system, predictable, that is, in a rough, general sense; for, of course, it has required much scientific imagination to discover these correlations and it will involve a great deal of tedious work to evaluate the degree of the interrelation. Now, may not the relative magnitudes of morphological features be a reflection of, or be quantitatively associated with, the plant's ability to carry on its life processes, *i.e.*, the physiological processes that we find such difficulty in measuring? If morphological characters have

physiological bases, may not morphological correlation be associated with physiological correlation?

In this we come to the root of the matter. The attention of plant physiologists has ostensibly been directed chiefly to the relations between plant and environment. I say ostensibly because, although the environment is measured as such, the plant is not. The plant is always measured in terms of the results of the interaction between environment and plant. We have no word for the plant itself, its inherited potentialities, the features that make it an individual. We know that plants of the same species, variety, and crop are physiologically different and remain so all their lives. These quantitative differences we vaguely ascribe to "individual variability," and on it we blame many, if not most, of our experimental difficulties.

To present the matter from another standpoint and thus, perhaps, make it clearer: suppose we could measure this internal, physiological constitution of the plant, that we knew all there was to know about a plant's *ability* to operate. Suppose we allowed these plants to grow in hermetically sealed boxes, of various sizes, shapes, and contents, the contents being wholly unknown. Suppose that after an interval of time we should analyze the contents of the boxes by every means at our command. How much knowledge would be acquired regarding the plant's relations with its environment? How much of the content of the box was put there by the plant and how much was residue? What compounds were formed by the plant and what by interaction of plant excretion and box content? How many repetitions of the experiment would be necessary before sure knowledge would be gained? True, we might select the boxes as to uniformity of size, shape, color, etc., but what would that avail if there were no relation between externals and internals? Now, restate this, replacing the words box and box-content by plant, and *vice versa*, and we have a picture of the present situation.

It must be evident that the saving feature in the case of the measurable environment and the unknown plant, the situation in which we actually find ourselves, is that there *is* a relation between externals and internals, and that a plant's activities do not have an indefinitely large range but are limited. Why then do we have so much difficulty in ascertaining the relation between environment and plant? In the absence of a problem's solution no one, of course, can state all reasons for failure to find one, but there are considerations that offer probable answers to the question. In the first place, the environment has not been completely stated in any instance, nor consciously duplicated in any two instances. Accordingly, the situation is more complicated than the term "measurable environment" might seem to indicate. As has so many times been pointed out, it should be measured and controlled—and if I may interject a remark, a first-hand acquaintance with the first story of the physics building is required for this: a precise workable equipment of laboratory knowledge.

In the second place, since we have little knowledge of the relations within the plant, of the interrelations of the plant's activities, even in an environment whose composition is measured, but which in kind and quantity of components is chosen at random, there is little chance of success because the main current or trend of the plant's activity may, and surely does, change if the environment is sufficiently altered, or altered in particular respects. We know enough on this point to be sure that such an altered activity is common. In the third place, since we select our plants on the basis of the magnitude of an external character such as height of seedling at a certain age, weight of seed, color of seed, etc., and not on the basis of a *relation* between external characters, we are again dealing, not with the plant's internal constitution but with the product of the interactivity of environment and plant, even though that interactivity occurred before the materials came to hand, that is, during seed formation. This should be taken to indicate, not that work of this kind is without value, but that it would progress more rapidly and more surely if the ever-present variable of plant constitution could be evaluated.

This brings us to another objection. Suppose for the sake of argument, it may be said, that internal activity and external character are related quantitatively, does it follow that the relationship is either direct or easy of discernment? Of course not; if the relationship were direct and easy it probably would have been noticed long since. Hope lies in the general success of such endeavors in physics and in physical chemistry, but this point of view is not proposed as a panacea for all experimental difficulties; it is a proposal for a campaign rather than for a *coup*. A little later I shall attempt to consider an avenue of approach, general considerations upon which methods may be based, and this will probably prove a more satisfactory form of answer.

It has been objected that, even supposing we have found a mathematical expression connecting the activities of a small number of individual plants with their measurable characters, such a relation must involve one or more constants peculiar to the individual, and since these constants will vary in magnitude from individual to individual over an enormous range, the information obtained from the expression could not be applied to a large assemblage of individuals, such as a field of wheat. This does not seem to offer a real difficulty at all. We have information now at hand to furnish the probable answer—which is that the information *could* be applied. Physiology is proceeding on a general conviction that contradicts this objection. The success of the statistical method, the success attending the use of the average in physiological work, both evidence that physiologists firmly believe that, if a sufficient number of individuals be considered, the changes in the results produced by adding more individuals will be negligible. In other words, characteristics are not variable through an infinite range, nor irregularly through a limited range. On the contrary,

the distribution of characters is so ordered that by plotting numbers of individuals with a like magnitude of activity-intensity under a given set of conditions as ordinates and the corresponding magnitudes as abscissas, a curve of distribution will be obtained, a curve which has a form characteristic of the kind of activity considered and which will be unchanged by incorporating data derived from other individuals, if a sufficiently large number were considered in the first place. If, instead of the magnitude of an activity, the magnitude of the constant were thus to be plotted, there is every assurance that a curve of characteristic form would similarly be produced and, moreover, the value of the constant for the average individual could thus be determined. Naturally a sufficiently large number of individuals must be investigated, but the difficulties would be less than they now are for statistical investigation of the effect of environment upon plants, for the experiments need not be performed upon all the plants at the same time. As a matter of fact, they need not be performed under precisely the same experimental conditions, for, within limits of course, the constant characterizes the plant under all external conditions without change.

In this lies a further great advantage that will accrue to physiology. Many experiments of fundamental importance to the science are not begun because of the virtual impossibility of performing difficult or tedious operations upon a sufficiently large number of plants. In other experiments the mere collection of the required data destroys the plant. If the proper relations of the kind we are discussing were known for the physiological processes under consideration by an experimenter, many of the difficulties that hamper him would vanish. A few plants operated upon in the desired fashion would yield data that in conjunction with our plant constant would permit the extension of the conclusions to the average plant or to any individual whose constant was known. Plants need not be destroyed to ascertain the progress of some process not accessible to direct observation in the living plant, for successive measurements of a change in the externally manifested variables would permit the calculation of the corresponding changes in the internal activity.

It will be promptly objected that one of the outstanding characteristics of plants is their ability to alter their habit of living, to become really different systems, and hence to change their constants. This is actually an argument for undertaking the determination of these constants, because, whether the constant turns out to be useful or not in practical experimentation, this question of the degree of stability of inherited characteristics is fundamental to a unified science. At present plant physiology is much in the condition of chemistry before the discovery of combining weights: no theoretically valuable, quantitative experimentation was possible. Without question the greatest handicap under which plant physiology—and all biology—labors is the inability of the experimenter to evaluate the organism with which he works.

Having indicated some of the general benefits likely to accrue from the application to physiology of that clause in the physicist's creed that expresses belief in the quantitative relationships existing among the various characteristics and attributes of a material system, we may turn to an example of this clause as a means, perhaps, of making the idea more concrete. I refer to a principle proposed by Le Chatelier[3] and by Braun,[4] and often termed Le Chatelier's theorem. This principle states that all systems are conservative, or, *in extenso*, "Each change in an outer condition that affects a body or a system produces in it a change in such a direction that as a result of this change the resistance of the body or system to this outer change is increased."[5] This law, so far as physics and chemistry are concerned, is perfectly general, indeed it is embodied in the second law of thermodynamics, and there is thus additional reason for believing it to be operative in biology.[6]

Biologists long since adopted as a fundamental principle of their science what seems to be the same law stated in biological terms: they said that organisms tend to adapt themselves to changes in their environment. If an outer condition affecting the plant is altered, the plant alters within itself in such a way as to adjust its activities to the new state of affairs and to maintain recognizably its individuality.

It must now be noted that the Le Chatelier-Braun theorem implies always a connection between the directions of *two* processes that may occur in the body or system. If one of the processes is known, the theorem indicates the necessary existence and the direction of action of a second process.[7] It is with this connection that we are concerned today rather than with the theorem itself: that there is an interrelationship of plant processes which should be statable mathematically. This corollary should be as nearly universally true as the theorem itself.

It should be further noted that the "outer condition" of the theorem need not be outside the plant, for, since energy transformations occur inside the plant, portions of the plant may be "bodies or systems" in the sense of the theorem and be affected by changes in other conditions within the plant; the theorem is concerned with the energy relations of processes and their determining conditions, which are, in turn, expressions of other processes, and not with their spatial arrangements. Thus the introduction of a coil of wire between the poles of a magnet calls forth energy readjust-

[3] Le Chatelier, H. Sur un énoncé général des lois des équilibres chimiques. Compt. Rend. Acad. Sci. Paris **99**: 786–789. 1884.

[4] Braun, F. Untersuchungen über die Löslichkeit fester Körper und die den Vorgang der Lösung begleitenden Volum- und Energieänderungen. Zeitschr. Physikal. Chem. **1**: 259–272. 1887.

[5] Chwolson, O. D. Lehrbuch der Physik **3**: 475. Übersetzt E. Berg. Braunschweig, 1905.

[6] For discussions of this theorem from biological standpoints see Hooker, H. D., Jr. Behavior and assimilation. Amer. Nat. **53**: 506–514. 1919, and the literature there cited.

[7] Chwolson, O. D. *Loc. cit.* 475, 476.

ments in açcord with the theorem regardless of whether or not both coil and magnet are parts of one structural entity, a dynamo; indeed, the magnet may be excited by a part of the current induced in the coil and thus coil and magnet have part in another process. It is the thesis of this paper that these *internal interrelations of processes are denoted in biological terminology as correlations*, which are thus seen to be not biological peculiarities to be considered merely as interesting phenomena but manifestations of the operation of an ordered universe to be investigated for the light they may shed on the plant as a reactant.

So far the discussion has been vague with respect to the kind and number of variables that must be considered. Of course, since there are no rules to guide us, correlations and their mathematical relationships may be looked for among any characteristics of the plant. No one can say that random search would be barren of result. But since we have a somewhat extensive list of correlations already observed, which seem to have some physiological significance, it would seem to be the part of wisdom to begin with these. The Le Chatelier-Braun theorem plainly indicates a functional relation between the connected variables. A first-hand acquaintance with the general deductions of plant physiology should thus be a guide. Naturally, as the body of this sort of knowledge increases, relationships hitherto unsuspected will probably appear and, in their turn, lead to new ideas regarding the mechanisms of functional adjustment.

One must be constantly on guard, however, not to infer that use of the same term in two cases indicates real correspondence of function. The word *growth* is such a term. It is common, for example, to use dry weight of plants as a measure of growth and to use increase in size as likewise indicative of growth. Dry weight has been an elusive quantity to say the least, perhaps because it is made up of varying proportions of differently usable substances, but at any rate it would seem on purely physiological grounds that both terms should not be directly and positively indicative of the same thing. Respiration is a fundamental activity of plants. Enlargement is also. Put a plant in a situation that permits these two processes to proceed but that prevents additions of substances contributing to the dry weight, and the plant will enlarge and respire at the expense of compactness of solid substance. The more actively a plant or a tissue respires and enlarges the less compact is its solid matter. This is a matter of common observation. It would seem then that the plant's dry weight is but the material unused in respiration and enlargement and should not, by its mere magnitude, be taken as indicative of conditions favorable to the individual plant itself, although the value of dry weight to its offspring or to mankind may be large.

Regarding the number of variables to be considered, it would seem that these should be taken, not as two, as is usually done in correlation studies, but as three, for this seems to be a necessary consequence of the Le Chatelier-

Braun theorem.[8] The discovery of the third variable may furnish the key to some of those sets of graphs, the curves of which exhibit so marked a tendency toward synchrony in the occurrence of their maxima and minima—a correspondence that is evident only upon casual inspection and which vanishes upon detailed examination, leaving one with the perplexed feeling that *some* relation exists. Possibly dry weight, enlargement, and respiration may be three such variables, dry weight being considered as indicated above, although the choice of proper units will involve difficulties. This must be done, however, with individuals, not statistically, if such a relation is sought.

Thus far may we be carried by the discussion of properties of systems as a point of view. Further progress, aside from filling in the gaps in this outline, initiates the consideration of particular problems and correspondingly particular methods. There is always danger in discussing generalities and avoiding the concrete, and, lest the whole matter be thought of as still in the nebulous state of a day-dream, it may be well to state that a beginning has been made[9]—a beginning which, although modest in its comprehensiveness, seems to increase in possibilities and exactness the further it is carried. I do not present the data or the method for two reasons. First, it seems that a presentation of the general point of view would have to be made anyway and is, indeed, of vastly greater importance than a presentation of one of its applications. Leaving the mind undistracted by numerical data and their symbolic representation may allow some one to apply the general principle to problems upon which he is engaging himself, instead of inducing him to regard the matter as a problem in a field foreign to his own. The second reason is obvious: lack of time.

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[8] Chwolson, O. D. *Loc. cit.* 476–480.

[9] Some of the early results were presented before the Physiological Section of the Botanical Society of America at its Baltimore meeting in 1918, under the title, "Growth equilibria in *Pinus Strobus*."